Notes on the Nephridia of Dinophilus and of the Larvæ of Polygordius, Echiurus, and Phoronis.

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With Plate 8.

In this paper are recorded some observations made on four different types of true nephridia provided with closed internal ends bearing some form of solenocyte. Although all these nephridia have been more or less completely described at some time or other by various authors, I am able to add some details, not without interest, which help to complete our knowledge of these organs.

Dinophilus.

The nephridia of this free-swimming Annelid have been described by Schmidt, Korschelt (**7**), Meyer (**9**), Harmer (**5**), Schimkewitsch (**11**), and Shearer (**14**). It is stated by Korschelt that in D. apatris, and by Meyer that in D. gyrociliatus, the internal extremity is blind, and ends in a flame cell. In Harmer's excellent account of D. tæniatus the end is said to lie in a cavity near the gut, and to bear a ciliated appendage or knob forming the base of attachment for the flame-like bunch of cilia which beat down the lumen of the canal. Harmer is not positive as to the absence of an opening.

In 1906 Shearer made the interesting discovery that the "ciliated appendage" of Harmer is really formed of a number of solenocyte tubes, comparable to those I have described in

many Polychætes. These tubes had already been indistinctly seen and described by Harmer as "elongated, pear-shaped bodies" which "vibrated individually."

The blind internal end of the nephridium of D. tæniatus ends in a bundle of blind, slender tubular extensions, at the extremity of each of which is attached a long flagellum. The flagellum works down the tubule into the lumen of the nephridial canal, which is not otherwise ciliated.

While able fully to confirm these important observations made by Shearer on the living worm, I am also in a position to complete his description from sections of well-preserved material.

Fig. 1 is a slightly diagrammatic reconstruction, from sections, of the end of the nephridium. These structures are very small, and can only be made out with the highest powers. The nephridial canal is relatively thick-walled; the cells of which it is composed are loaded with excretory globules and pierced by an intra-cellular lumen. Nuclei can be seen at rare intervals along its course. One conspicuous large nucleus is always found at the extreme end, which projects into a free space, supported by strands of mesenchymatous tissue. Here the nephridial lumen expands into a chamber bounded on one side by a thin wall from which arise the "solenocyte" tubes. They may be considered as hollow outgrowths of the wall. In sections they appear rather shorter and stouter than in the living worm; this is probably due to contraction of the preserved material. Each tube bears a little lump of protoplasm at its free extremity, from which starts the flagellum. No nuclei are found on or near the tubes themselves. The whole apparatus thus consists of a single cell bearing some twenty or thirty tubes and flagella, all controlled by the one large nucleus mentioned above.

It is clear that in Dinophilus we have a new type of solenocyte formation representing perhaps an intermediate step between the Platyhelminth "flame-cell" and the more typical Polychæte solenocyte, in which each tube, with its

flagellum, has its own nucleus. This latter state might be reached by a multiplication of the nuclei until they came to correspond in number with the tubes. That Dinophilus is related to Polygordius has long been suspected; it is therefore interesting to note that in the larval nephridium of Polygordius there is a similar multiplicity of tubes, as I showed some years ago (**2**).

The Larva of Echiurus.

It is to Hatschek that we owe the first detailed description of the larval nephridia of Echiurus (**6**). According to his account there are a pair of larval nephridia without internal opening. In the late larva there is a membrane separating the cœlom near the gut from a space below the body-wall traversed by mesenchymatous strands. Hatschek describes the nephridium as passing inwards from its external pore through this space, to spread out in a system of fine branches on the outer surface of the membrane. The nephridium ends in "ein Büshel von Endorganen," and "die Endknöpfchen der feinsten Canälchen je einen Zellkern enthalten."

This description and the accompanying figures had long led me to suspect that the "Endknöpfchen" were in reality "solenocytes." It was not, however, till this spring that I had an opportunity of confirming my suspicions by the examination of living larvæ at Naples.

Fig. 3 is a careful drawing from life of the nephridium of a larva of about the age shown in Hatschek's fig. 4. A glance at my figure shows that the nephridium is, in fact, provided with typical solenocytes. The canal leading from the external pore has granular, rather thick walls; when it reaches the membrane outside the cœlomic epithelium it divides into a number of thin-walled branches, which spread over the membrane. These terminate in delicate, almost cylindrical tubes, at the end of which are the nucleated cell-bodies. The nuclei can be seen even in the living state.

As figured by Hatschek, fine protoplasmic threads extend

from the cells, by means of which they are attached to the surrounding structures. From each of the cell-bodies a long flagellum passes down the tube into the canal of the nephridium almost to the external pore. A few similar but shorter flagella spring also from the wall of the canal itself. Sections show that the lumen is intra-cellular, that nuclei are present in the wall of the duct leading to the pore, but absent in the fine branches. It is interesting to find that the solenocytes project freely both into the mesenchymatous spaces on the outside of the membrane, and into the cœlom, passing through the cœlomic epithelium.

We may now add the Echiuroidea to the already long list of groups in which are found typical solenocytes.

What may be the origin of the anterior kidney tubes of the adult Echiurus is still quite unknown. Obviously they are not derived from the larval organs, which open much farther forwards in front of the large paired setæ. Hatschek (**6**) and Salensky (**10**) have given some account of the development of the posterior so-called anal kidneys, and these appear to be not nephridia at all, but cœlomoducts derived from the cœlomic epithelium. The more anterior kidneys of the adult are probably of the same nature. I may add that I have found no trace of the supposed opening of the duct of the larval nephridium into the cœlom mentioned by Salensky.

The Actinotrocha Larva of Phoronis.

In a paper published in 1903 (**3**) I was able to show that the larval nephridia of this larva project into the hæmocœle, where they end blindly in bunches of solenocytes. It is unnecessary for me to repeat here this account, or to again refer to the older literature on the subject. But attention may be drawn to several papers since published. Cowles (**1**) and De Selys Longchamps (**12**) have confirmed most of my statements with regard to the structure of the nephridium. Moreover, De Selys and Cowles agree with Ikeda (**8**) as to the origin of the nephridia from an ectodermal pit. But it

is to Shearer (**13**) that we owe the first clear and definite account of the development of the solenocytes themselves. They arise from the wall of the ectodermal pit, as is convincingly shown in his figures.

During a visit to Helgoland last year I was able again to study the nephridium in a living Actinotrocha larva (A. branchiata). In this form it is a large organ with a branched internal end lying in the preseptal hæmocœle. As shown in fig. 4, multitudes of solenocytes project from the wall of the nephridial canal. The nuclei are placed, not at the extreme end of each tube, but rather at the side. Now it is well known that an accumulation of blood-corpuscles is generally found in the immediate neighbourhood of the nephridium in these larvæ, and the interesting new point I have to bring forward is this—that very long, stiff cilia are set among the solenocytes, attached by their base to the wall of the nephridium between the solenocyte tubes.

Although I did not observe these cilia move very actively in the larva compressed under a cover-slip, yet I have little doubt that they agitate the blood-fluid, and so lead to the gathering of the corpuscles just mentioned. I have described almost exactly similar cilia on the nephridia of the Alciopids (**2**), but in these Polychætes they lie, of course, in the cœlom. Actinotrocha is the only form, so far as I know, in which they occur on a nephridium projecting into a hæmocœlic space.

The Larva of Polygordius.

Since the figure of the nephridium of a larva from Ceylon published in 1900 (**2**) was based on somewhat doubtful observations made on scanty material, I have here given a new and more complete representation of the whole organ (fig. 2) as it occurs in the Neapolitan species. The drawing was carefully made from the living larvæ of about the stage shown in fig. 8, Pl. 11, of Fraipont's well-known monograph (**4**). It will be seen at once that the new figure confirms in every respect the account I previously gave, in which it was first shown

that the blind internal extremities are provided with solenocyte tubes.

The stiff refringent solenocyte-tubes run free from the protoplasm of the umbrella-like web, and are attached to it only at one end, which may be called the outer end. The opposite end of the tube plunges though the wall of the nephridial canal, into which it opens. The flagellum passing down the tube into the nephridial lumen is of remarkable length. Thickened protoplasmic ridges pass radially along the web from the central mass to the periphery, where they embrace the outer extremities of the tubes. The apparatus may be either expanded or contracted, as can be seen in the figure. In the expanded condition the web is flattened out with the tubes widely diverging; the central mass and contained single nucleus then lies somewhat flattened in the middle. When the web closes up, the tubes are on the contrary drawn together until they become almost parallel, and the central mass with its nucleus is made to bulge outwards as a convex knob.

There is no doubt, then, that in P. neapolitanus a single nucleus, at the tip of each branch of the nephridial canal, controls a set of from six to seven solenocyte tubes. If Woltereck's recent description of the nephridium of a North-sea larva is correct, it would appear to differ considerably in structure; for he states that there is a nucleus to each tube, that the tubes are covered by the cytoplasm, and figures no web between them (**16**). In an important paper on the development of Polygordius, Shearer (**15**) has given a most careful account of the origin of the larval nephridia; they arise from two cells differentiated quite early, lying on the inner surface of the ectoderm, and probably derived from it. Each of these cells multiplies to form a chain which develops into the whole nephridium. The solenocytes arise from the extremity of the nephridium itself. These observations entirely confirm the view that the canal and solenocytes of the Annelid nephridium form a whole, a single organ derived from one rudiment, strictly comparable to the canal and flame-cells of the platyhelminth excretory organ.

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EXPLANATION OF PLATE 8,

Illustrating Mr. E. S. Goodrich's "Notes on the Nephridia of Dinophilus and the Larvæ of Polygordius, Echiurus, and Phoronis."

Reference Letters.

b. c. Blood-corpuscles. *c.* Cilium. *c. m.* Central mass of cytoplasm containing a single nucleus. *c. t.* Connective tissue. *fe.* Flagellum inside the solenocyte tube. *n.* Nucleus. *n. c.* Nephridial canal. *np.* Nephridiopore. *pr.* Cytoplasmic process. *prm.* Mass of cytoplasm at end of tube. *s.* Septum separating the cœlom from the hæmocœle in which lie the solenocytes. *t.* Tube of solenocyte. *w.* Thin cytoplasmic web.

Fig. 1.—Restoration from sections of the inner end of the nephridium of Dinophilus tæniatus. The organ is represented as if cut longitudinally.

Fig. 2.—Drawing from life of the whole nephridium of the larva of Polygordius neapolitanus.

Fig. 3.—Drawing from life of the whole nephridium of Echiurus sp.

Fig. 4.—Drawing from life of the inner end of the nephridium of Actinotrocha branchiata.